

Willow Warbler *Phylloscopus trochilus* imitating the song of the Chiffchaff *P. collybita*

by Svein Haftorn

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A mixed singer of the genus *Phylloscopus*, most probably a Willow Warbler *P. trochilus*, was observed and tape-recorded at Heimdal (63°19'N, 10°21'E) close to Trondheim in central Norway in July 1983. A similar songster, probably the same individual, had claimed the same territory also in the previous year. The bird sang a pure Willow Warbler song (most commonly), a pure Chiffchaff song (less frequently) and a mixture of the songs of both species. It nearly always started with a varying number of Chiffchaff figures, which without any pause were followed by a final part of the Willow Warbler song. The immediate impression, that the Chiffchaff figures were bewilderingly similar to those of an authentic Chiffchaff, was fully confirmed by sonagram analyses, although the bird sang at a significantly higher speed.

For more than a hundred years it has been known that warblers of the genus *Phylloscopus* occasionally sing songs which are more or less a compound of normal Willow Warbler song and normal Chiffchaff song (see Tiainen 1991 and references therein). Understandably, some doubts were raised about the identity of such singers, whether they were genuine Willow Warblers or Chiffchaffs, or hybrids between these two species. Schubert (1969) reviewed the literature on this topic and came to the conclusion that the birds concerned were neither hybrids nor Chiffchaffs, but Willow Warblers that had learned the song of the sibling species. The mixed singers always lacked the typical, faint *trett* calls, which the Chiffchaff often utters during the pauses between songs. Another transcription of this call is *tirre* (Haftorn 1971), to indicate that it in fact is disyllabic (Fig. 1a).

More recently, Haensel & Lippert (1976) described a German mixed singer which they determined without doubt ("einwandfrei") as being a Chiffchaff, on account of morphological characters and the presence of species-specific *trett* calls between songs. Furthermore, in Ireland, Wilson (1986) observed a Chiffchaff mixed singer, the specific identity of which was established by trapping and ringing.

In a few cases "mixed singers" have been tape-recorded and their songs analysed by means of spectrographs (Schubert 1969, Haensel & Lippert 1976, Helb *et al.* 1985, Wolf 1986). In the present paper I describe the first known record of a mixed singer in Norway and probably the second record for Scandinavia as a whole. In April 1990 a mixed singer, that exhibited all the important characteristics of a Chiffchaff, was detected at Ängelholm, Scania, in Sweden (Fritz & Hernborg 1990).

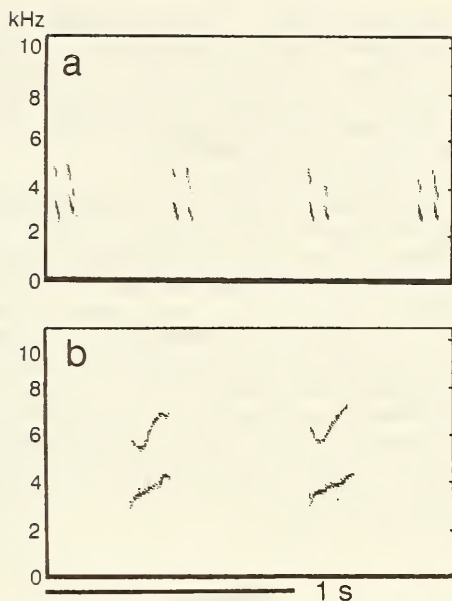


Figure 1. (a) The faint and dry *terr* or *tirre* sound, which the Chiffchaff frequently utters during the interval between songs (Klaebu, 28 June 1967). (b) The corresponding sound of the Willow Warbler, a soft note, which is inaudible at a distance, just as the Chiffchaff's *tirre*. The two calls depicted were given by the mixed singer at Heimdal (13 July 1983) between two songs. The same call is also seen as an introduction to the mixed song in Fig. 4.

Material and methods

In July 1983, Karl G. Larsson drew my attention to a peculiar Willow Warbler in the suburb of Heimdal (63°19'N, 10°21'E) close to Trondheim, in Sør-Trøndelag province in Central Norway. According to this observer the bird sang the song of the Chiffchaff in addition to its specific song. A bird with a similar song pattern, most likely the same individual, had been observed in exactly the same locality the previous year. However, it did not return in 1984.

On 17–18 July 1983 I watched the bird for several hours and tape-recorded the song. It claimed a rather small territory, comprising gardens with lawns bordered by spruce and deciduous trees. I heard Chiffchaff song in the vicinity and, some distance away, a Willow Warbler's typical song. According to Larsson, the Willow Warblers were clearly outnumbered by Chiffchaffs in this area.

The bird behaved like a typical Willow Warbler and sang when either sitting in the crown of a spruce or while foraging in the bushes and trees within its territory. For long periods at a time it uttered pure Willow Warblers songs (type 1), but then, at irregular intervals, it suddenly gave forth mixed songs with either figures of both species

(type 2), or, though more seldom, typical Chiffchaff songs without any components of the Willow Warbler song (type 3). I tape-recorded 111 songs of type 1, 83 of type 2 and 16 of type 3. These totals do not reflect the true frequencies of the three different song types, however, because I deliberately selected periods during which the bird was inclined to incorporate figures from the Chiffchaff song.

The individual observed was not captured and its specific identity could therefore not be established from morphological characters. Two traits, however, provided good evidence that it was a Willow Warbler. Firstly, the frequency of normal Willow Warbler song was far higher than that of songs including Chiffchaff figures. Secondly, the bird never incorporated the *tirre* call, which is so typical for the song of the Chiffchaff. On the contrary, it used instead a faint *ui* note (Figs 1b and 4; see also Fig. 2c), which the Willow Warbler occasionally utters in the pauses between its songs and which seems to be species-specific. This *ui* note is probably homologous with the *tirre* call of the Chiffchaff.

The song was recorded using a Sony TC-D5 PRO recorder, fitted with a Dan Gibson reflector, and was analysed on sound spectrographs (Voiceprint ser. 700, and Uniscan II with hardcopy digital sonagrams printed on Epson FX-85 printer).

Results

As already mentioned, the bird's song repertoire contained three main versions: (1) the normal Willow Warbler song, which dominated its repertoire, (2) mixed song, which ranked second in numbers, and (3) pure Chiffchaff song, which definitely was the one most rarely performed.

Normal song

The normal song of the bird was of the 'spontaneous' type, i.e. that delivered in undisturbed situations (Fig. 2d-e). I never heard the "A-song" (sensu Järvi *et al.* 1980) used during territorial combats. Because the bird was not involved in any agonistic situation during my stay, performance of the A-song was unlikely in any case. For comparison, Figure 2a-c shows various types of 'spontaneous' songs of Willow Warblers from two other Norwegian breeding localities.

Mixed song

Mixed song consisted of parts of the song of the Willow Warbler and the Chiffchaff combined (Fig. 3). It nearly always started with the Chiffchaff song (sometimes very few figures as shown in Fig. 3d) and then it suddenly, without any break, switched to a final part of the normal Willow Warbler song. Thus, the complete Willow Warbler song was never incorporated into a mixed song. The bird simply replaced the first part of the conspecific song with figures taken from the Chiffchaff's song. The song length was apparently the same as that of its normal song (means 3.8 ± 0.61 s, $n=20$, and 3.5 ± 0.82 s, $n=21$, 2-tailed Mann-Whitney U-test, $P=0.19$).

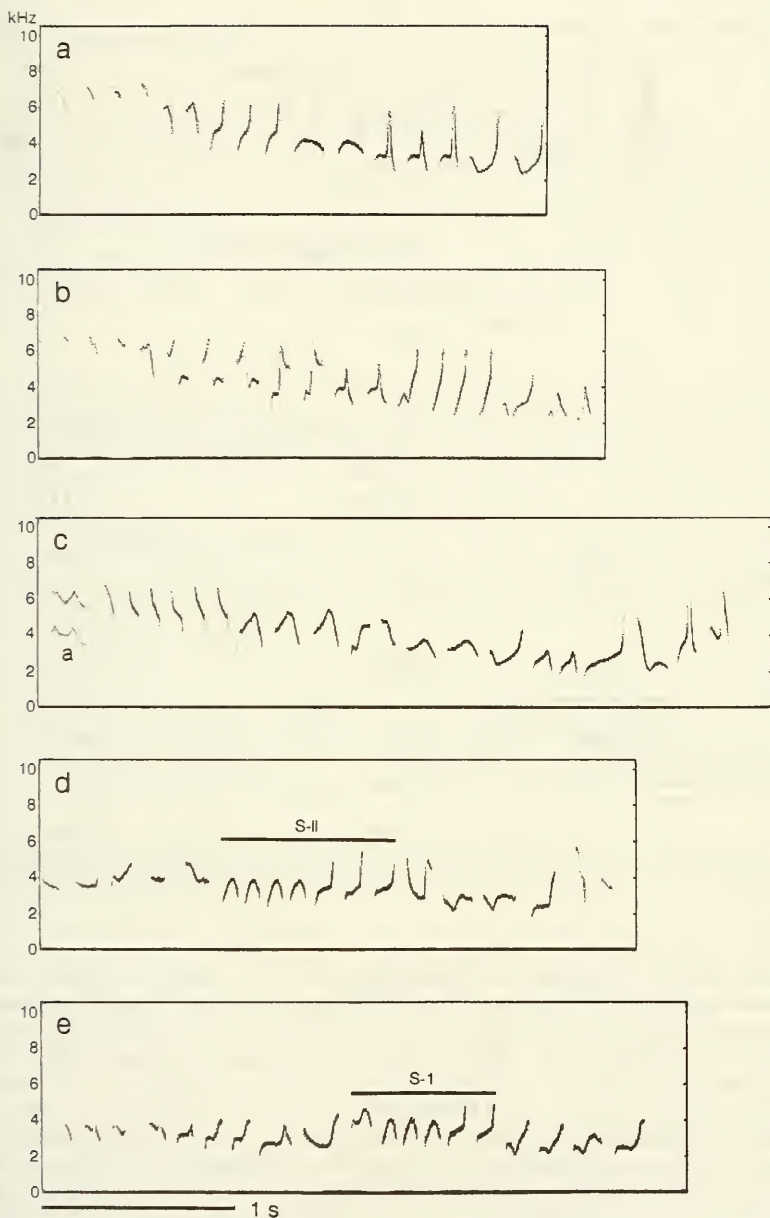


Figure 2. (a–b) Two types of full song by one and the same Willow Warbler (Klaebu, 18 May 1992). (c) Song by another Willow Warbler (Venabu, 24 June 1990). Notice the faint introductory note (a), which is homologous to the 'interval signal' shown in Fig. 1b, although somewhat different in shape. (d–e) Two versions of pure Willow Warbler song given by the mixed singer at Heimdal (13 July 1983). S-I–S-II=syllables I–II (see text).

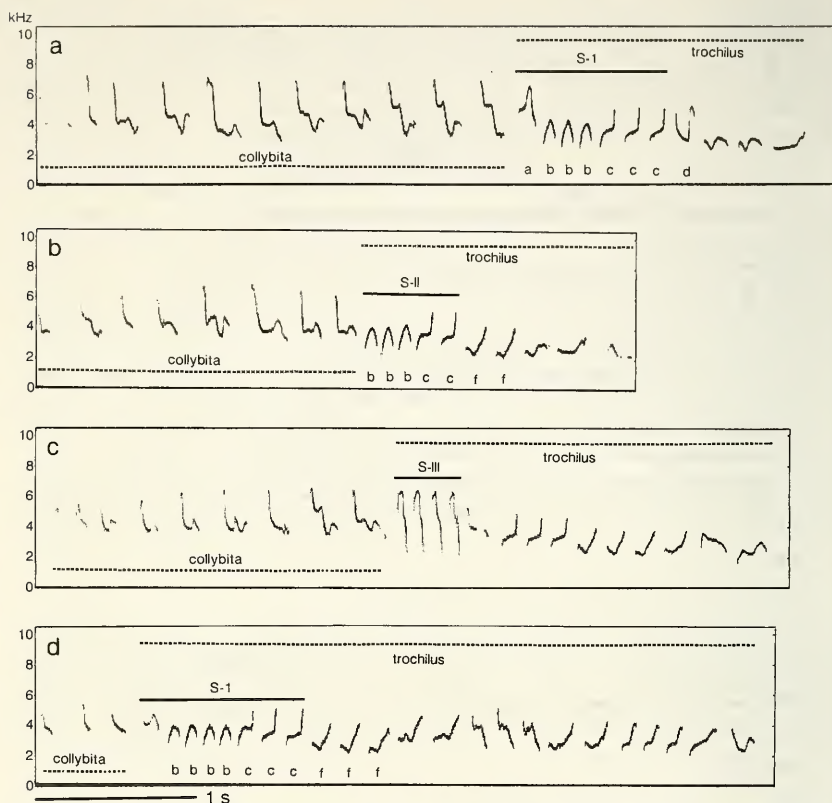


Figure 3. Four examples of mixed song given by the mixed singer at Heimdal (13–14 July 1983), starting with Chiffchaff figures and ending up with an abbreviated song of the Willow Warbler. See main text for further information. S-I–S-III=syllables I–III (see text).

The initial figures in the mixed song were usually incomplete and uttered very softly (as in normal Willow Warbler song), but then increased rapidly in loudness and became Chiffchaff-like. The total number of figures occurring in this a-part for the song was most commonly 6–13.

According to Järvi *et al.* (1980), each male Willow Warbler possesses about 80 different song figures. The present mixed singer possessed at least 36 different figures, the Chiffchaff-like ones omitted. When, sooner or later in the song, the bird switched over to the Willow Warbler part, the initial figures in this b-part were not selected at random, however. It clearly favoured two syllables, which were distinguished only by the first figure. The syllables I and II in Figure 3a, b were chosen in 30 and 24 instances, respectively, out of the total of 83 mixed songs recorded. A third syllable (III in Fig. 3c) was used only 6 times, whereas a variety of

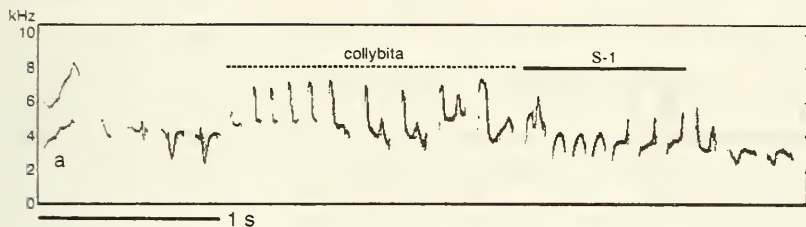


Figure 4. A series of Chiffchaff figures inserted in Willow Warbler song of the mixed singer at Heimdal (13 July 1983). The very first note shown (a) is a typical "interval signal" (see Fig. 1). The first figure in S-I is somewhat aberrant (cf. Fig. 3a).

figures opened the b-part in the remaining 23 mixed songs. The figures comprising the rest of the b-part varied somewhat in structure from one song to the next, the whole phrase descending in pitch and fading away in the usual species-specific manner. Quite often, however, the syllables I and II were followed by the figures d (Fig. 3a) or f (Fig. 3b,d). The overall impression was that the bird just copied a version of the final part of its normal Willow Warbler song. But a close study revealed that the syllables I and II did not appear nearly as often in the bird's normal song as they did in the mixed song; the respective proportions were 23.4% and 65.1% ($\chi^2=34.0$, $P<0.001$).

Only rarely did the bird deviate from the pattern described. Twice it started with the normal Willow Warbler song and then terminated with one Chiffchaff-like figure, and twice one and 10 Chiffchaff figures, respectively, were inserted into normal Willow Warbler song. In the latter case the character of the Chiffchaff song was almost lost because of the rapid sequence of figures (Fig. 4).

Copies of pure Chiffchaff song

Songs composed of pure Chiffchaff-like figures were recorded only 16 times. The first figures in each song were usually softer than in genuine Chiffchaff song (thus maintaining a marked Willow Warbler trait), but the rest of the song was extremely Chiffchaff-like (Fig. 5). Except for the hook on top of several imitated figures it is hard to see any difference from genuine song. Similar hooks may also be found, although rarely, in true Chiffchaff song as well (Thielcke & Linsenmair 1963). In fact, every one of the seven minute characters found in the 'basic' Chiffchaff figure (see Fig. 4 in Thielcke & Linsenmair 1963) was exactly copied by the imitator. The pitch (approx. 4–7 kHz) and the amplitude of the imitator's song were also identical with normal Chiffchaff song. And, just as in genuine Chiffchaff song, the pitch and amplitude were kept at the same level throughout, in contrast to typical Willow Warbler song, which falls in pitch and fades away.

In one respect the imitator clearly differed from the Chiffchaff, however. It sang its song at a significantly higher speed (more figures per unit time) than any of the three Chiffchaffs with which it was compared (Mann-Whitney U-test, 2-tailed, $P<0.001$). On the other hand, the song

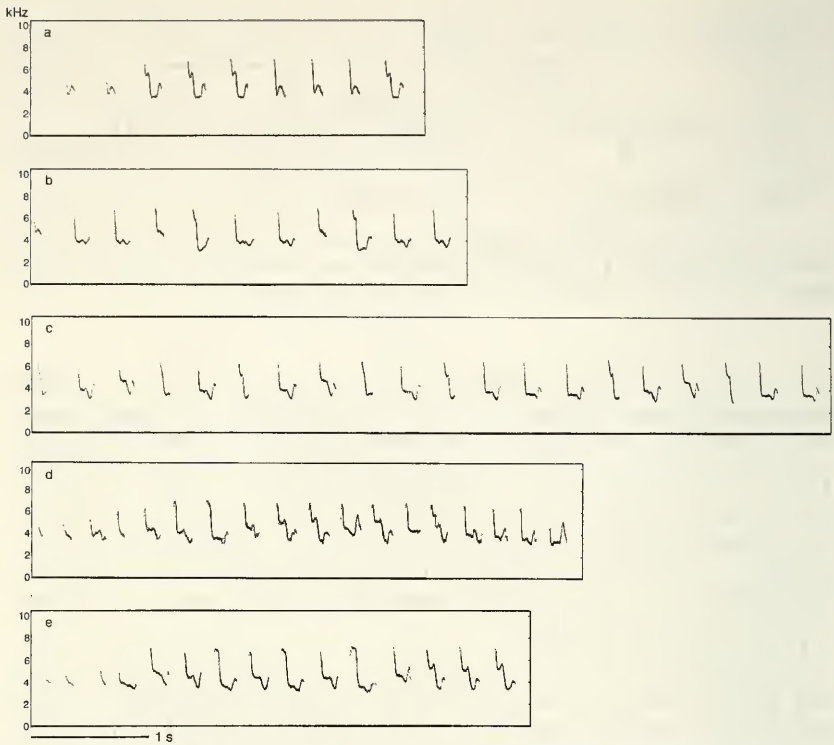


Figure 5. (a–b) Two songs of one and the same Chiffchaff (Klaebu, 18 May 1992). (c) Song of another Chiffchaff (Klaebu, 28 June 1967). (d–e) Examples of the mixed singer at Heimdal imitating pure Chiffchaff song (13–14 July 1983).

figures were delivered at a significantly slower rate than in normal Willow Warbler song, whether sung by the imitator itself ($P < 0.0001$) or another Willow Warbler ($P < 0.0001$). Hence, the speed of the imitator's pure Chiffchaff song was intermediate between true Chiffchaff song and normal Willow Warbler song. The speed depended on the duration of the intervals between the figures, not the length of figures.

Discussion

From the cases described in literature it appears that mixed singers of the Willow Warbler nearly always start with figures of the Chiffchaff song and then without break end up with the final part of the Willow Warbler song (Gwinner & Dorka 1965, Schubert 1969, Frost 1986, Wolf 1986). However, it occasionally happens that the birds reverse the order of song parts, or insert figures of the Chiffchaff in the Willow Warbler song (Schubert 1969, Wolf 1986, Tiainen 1991). The song of the bird described in the present paper, most likely a Willow Warbler

(see "Material and methods"), was in complete accordance with this song pattern.

Also two mixed singers identified as Chiffchaffs began their songs with Chiffchaff figures and terminated with Willow Warbler song (Haensel & Lippert 1976, Wilson 1986). A ringed Scottish mixed singer turned out to be a bird which two years earlier was brought up by a male Chiffchaff and a female Willow Warbler. Its intermediate morphological characters indicated that it was a hybrid (Prato & Prato 1986). Its unusual song "was best described as Chiffchaff-type phrases preceding and following typical Willow Warbler song".

Hence, it seems justifiable to conclude that the Chiffchaff and Willow Warbler occasionally copy each other's songs and utter the sibling song along with or mixed up with species-specific song figures. This situation makes the hypotheses put forward by Gwinner & Dorka (1965) and Schubert (1969), namely that the Willow Warbler might be phylogenetically younger than the Chiffchaff and genetically have preserved a predisposition to learn the Chiffchaff song, less likely. The two European species of Treecreepers, *Certhia familiaris* and *C. brachydactyla*, are also known to copy each other's songs (Thielcke 1960).

That the bird described here delivered Chiffchaff figures at a higher speed than in normal Chiffchaff song, seems to be typical of such singers (Gwinner & Dorka 1965, Helb *et al.* 1985). Gwinner & Dorka (1965) also noticed that the Chiffchaff-figures of the mixed singer had a higher frequency than in the normal Chiffchaff song. The present imitator, however, uttered its Chiffchaff song at the same frequency level as in normal Chiffchaff song (in Fig. 5 compare a-c with d-e).

There seems to be a common trend among mixed singers to start with patterns of the alien species' song and end up with parts of the conspecific song. Good examples are provided by (the imitator coming first) *Certhia familiaris*—*C. brachydactyla* (Thielcke 1960), *Anthus trivialis*—*Emberiza citrinella* (Helb *et al.* 1985), *Fringilla coelebs*—*Carduelis chloris* (Helb *et al.* 1985), *Geothlypis trichas*—*Dendroica pensylvanica* (Kroodsmas *et al.* 1983) and *Phylloscopus trochilus*—*Ph. collybita* (present paper).

Many species, including the Willow Warbler (Schubert 1976), are probably endowed with an innate 'auditory template' for learning their own specific song (see for example Slater 1989). Mixed singing could, according to Helb *et al.* (1985), be explained by "a temporary or permanent lack of a conspecific model together with exposure to an alien species during the sensitive phases of song learning". As these authors point out, a favourable condition for mixed song learning can be established when a species outnumbers its sibling species in an area of sympatry, which is in accordance with the numerical relationship between the Willow Warbler and Chiffchaff at Heimdal. Because of the numerical dominance of Chiffchaffs in this area (K. G. Larsson pers. comm.) a young Willow Warbler in its sensitive phase of song learning might have been tutored by neighbouring Chiffchaffs. Although the two species occupy almost mutually exclusive territories (Sæther 1983), it is likely that songs of Chiffchaffs are well within earshot of Willow Warblers reared in the area. Moreover, the Chiffchaff is an

extraordinarily vigorous songster with a very long song period, enhancing its chances of being heard by young Willow Warblers in their critical phase of learning. The prerequisite for this explanation is of course that the actual mixed singer was brought up at Heimdal or at another locality where Chiffchaffs are abundant. The first alternative is the less likely, because natal philopatry is very low in the Willow Warbler. At Polish, Finnish and Scottish control areas only 0–2% of the nestlings and 2–5% of the fledglings were recovered (Tiainen 1991).

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Address: Dr Svein Haftorn, University of Trondheim, The Museum, N-7004 Trondheim, Norway.